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Lack of Hand Preference in Wild Hanuman Langurs (*Presbytis entellus*)

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ABSTRACT Although there is a vast literature on laterality of hand-use in nonhuman primates, the Colobinae have been notably overlooked. Ten manual activities of differing complexity were studied in five male and five female adult Hanuman langurs (*Presbytis entellus*) from a well habituated, wild population at Ramnagar, in southern Nepal. The activities recorded were carry, eat, hit, hold, idle, manipulate, reach, retrieve, self-groom and social groom. This study aimed to examine handedness across tasks and across subjects in a natural population. The overall result was a lack of preference for subjects and patterns. Only in the eating activity did four individuals show significant hand preference, though they were not unidirectional. Eat seemed to be loosely associated with hold due to the requirements of the strata which the monkeys utilize. These results suggest that hand use is unlateralized in *P. entellus*. Those individuals exhibiting some hand preferences can be viewed as statistical exceptions or perhaps subject to experiential differences. The results are discussed in terms of their evolutionary significance and methodological implications. Am J Phys Anthropol 103:455–461, 1997.

Strong hemispherical lateralization is often considered a hallmark of the Hominidae and manual specialization is thought to be one of its best indicators. This is evidenced most clearly by *Homo sapiens*, whose consistent bias approaches 90% right-handedness (Marchant et al., 1995). However, the costs and benefits of hemispherical lateralization are not so clear (Marchant and McGrew, 1996), such that elucidating its evolutionary origins and possible uniqueness are important steps. Accordingly, research on lateralization in living nonhuman primates, especially the African apes, is needed (Marchant and McGrew, 1991; Hopkins and Morris, 1993).

A resurgence in studies of primate handedness was spurred by a critical review article by MacNeilage et al. (1987). They hypothesized that as a result of initial selection pressures centered around feeding and a move away from quadrupedalism, a left-hand preference for visually guided reaching, and a right upper limb specialization for postural support evolved early in primate phylogeny. This, they believe, led to population level handedness in nonhuman primates, though it is not clear why individual manual specialization would not have been just as useful.

Prior to MacNeilage et al., most studies had been limited to Cercopithecinae engaged in simple reaching for food. Recently, there has been a marked increase in the number of studies on great apes, especially

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as they exhibit the clearest examples of tool-use (e.g., Boesch, 1991). This tool use in turn agrees with Kimura's (1979) suggestion that hemispheric specialization for manual control in hominids evolved as an adaptation for bimanual coordination in the use and manufacture of tools. But, overall, the published literature on manual laterality is still limited to a relatively small range of primate species (Ward and Hopkins, 1993). A broader sampling of species is necessary to test comprehensively the competing hypotheses for the evolutionary origins of handedness (Byrne and Byrne, 1991).

Many studies of laterality of function have been done on lemurid prosimians (Forsythe and Ward, 1988; Ward et al., 1990). New World monkeys have been more overlooked and the existing results are ambiguous. Handedness was found in some cases (*Saguinus oedipus*, Diamond and McGrew, 1994; *Cebus apella*, Masataka, 1990) while only hand preference was found in others (*Cebus apella*, Westergaard and Suomi, 1993).

The Cercopithecoidea represent a phylogenetically, behaviorally, and geographically diverse group on which many handedness studies have been done. These studies, however, are problematic at various levels. As Fagot and Vauclair (1991) pointed out, almost all are restricted to the papionines, especially *Macaca mulatta* and *M. fuscata*. Moreover, as noted by MacNeilage et al. (1987, p. 248), "almost every study of Old World monkey handedness involves reaching and grasping a food reward." In a ranking scheme for food reaching related to task complexity (i.e., whether it was simple or complex; required exposing, stabilizing, or manipulating), MacNeilage et al. found that most of the cercopithecine studies used only simple reaching, and so did not elicit manual laterality potentially present within the species. Fagot and Vauclair (1991) separated tasks into low- and high-level and claimed that only high-level (or unfamiliar) tasks would produce asymmetry in distribution of lateral functioning both at the hemispheric and behavioral levels. That is, *simple* food reaching would not demonstrate manual specialization while complex visuo-spatial tasks would.

MacNeilage et al. (1991) further asserted that previous studies failed to detect nonhuman primate handedness because many of these studies did not specifically address factors by which a strong asymmetry would be evoked. These factors include: 1) field rather than captive studies, 2) tasks requiring visual discrimination, 3) tasks eliciting strong left-hand reaching preferences; 4) tasks eliciting right-hand manipulative preferences; 5) tasks measuring precision of manual control, 6) a relatively large number of tasks of varied complexity; 7) non-routinized behavior; and 8) adult rather than young subjects. The direct relation between increased manual laterality and age has been noted by many researchers (e.g., Fagot and Vauclair, 1991; Westergaard and Suomi, 1993).

Recent studies still do not address all these considerations. A study by Kubota (1990) on Japanese macaques (*Macaca fuscata*) reaching for food pellets found a left hand preference in 19 individuals, a right hand preference in 5 individuals, and 20 individuals with no preference. Although this study uses a fairly large sample size, it still utilizes non-adults as subjects, is a captive study, and uses a simple food reaching behavior to test for manual laterality.

Before our research, only two studies on colobines had been reported. Yuanye et al. (1988) looked at manual laterality in food reaching in golden monkeys and leaf monkeys (*Rhinopithecus roxellanae* and *Presbytis* sp.). No statistical details were presented, but for 25 *Presbytis* subjects, they reported 11 as right-preferent, 3 as left-preferent, and 8 with no preference. Neves and Dolhinow (1994) looked at simple food reaching in 13 captive Hanuman langurs (*Presbytis entellus*) that ranged in age from 2 years to 23.5 years. They found that 7 of the 9 adult monkeys were strongly lateralized either to the right or left. None of the infants was strongly lateralized. Thus, both existing studies focused on task specialization, not overall handedness.

In order to address as many of the inconsistencies as possible, and to extend research on the subfamily Colobinae, we studied 10 adult, free-ranging Hanuman langurs (*Pres-*

bytis entellus) performing a variety of behaviors of differing complexity.

METHODS

The research was undertaken through the Ramnagar Monkey Research Project. The study site lies 300 m above sea level in a deciduous forest of the Siwalik mountains, comprised mainly of Sal trees (*Shorea robusta*), near the village of Ramnagar, Chitwan District, Southern Nepal (27°44′N, 84°27′E) (Nikolei and Borries, 1997). Five male and five female adult Hanuman langurs were studied; each female carried a non-weaned infant. The subjects were members of a free-ranging multi-male, multi-female group (O-troop) composed of 5 adult males, 9 adult females, 4 young-adult females, 3 juvenile females, and 8 male or female infants.

The study troop was well-habituated, so that clear observation conditions (often within 1 m) were achieved, with the monkeys spending the greater part of each day on the ground and lower canopy during this time of the year.[1]

Observations were made daily from June 21 to July 26, 1995 between 0600 and 1800 hours by ESM. Each individual was observed using focal subject sampling (Altmann, 1974) in 20-minute sessions, for three "statistical days." A statistical day comprised a focal sample for each observation hour of the day for each individual (that is, 36 sessions per subject). Each individual thus had a total of 12 hours of sampling conducted on it over the course of the observation month. The order of sampling was randomly selected at the start of each statistical day. If a subject was not visible for more than 30 seconds of a focal minute, the minute was discarded and the missing minutes (not more than two) were added to the end of the sample.

The behavioral categories used to test the directionality of hand use are listed in Table 1. All behavior patterns were spontaneous and had to last for at least 5 seconds for it to be recorded (except Hit). A separate bout of the same pattern was only recorded if the hand broke contact with the original object of focus (object or individual) for at least 5 seconds.

TABLE 1. Behavioral categories and definitions

Category	Definition
Carry	Locomote while holding an object or infant
Eat	Pick up a food item (located within arm's length of its body) and place it directly into the mouth
Hit	Strike out with one hand toward another individual
Hold	Actively grasp an object or another individual
Idle	Hand not engaged in any behavior
Manipulate	Modify or otherwise handle an object, usually while it is held in the other hand
Reach	Extend hand to a distance greater than or equal to an arm's length toward an object or individual, but without grasping it
Retrieve	Reach to grasp an object or infant that is equal to or greater than an arm's length away and bring it closer to the subject
Self-groom	Hand used to start grooming own body
Social groom	Hand used to start grooming another individual

The orientation of the act (i.e., whether an animal performed a behavioral pattern to its left-side, right-side, or sagittal midline) was also recorded in order to control for this possible confounding factor to the observed direction of hand use. An animal's sagittal midline was considered to be within the space delineated by the shoulders of that animal. The object of the behavior was also recorded when applicable (e.g., hold fruit vs. hold branch). The data were analyzed statistically using a two-tailed Binomial distribution; the level of significance was set at $P \leq 0.01$.

RESULTS

The results show an overall lack of hand preference for individuals over behavioral categories except for Eat (Table 2). Nine of the 10 subjects exhibited no statistically significant degree of overall laterality over their compiled behavior and seven of the 10 categories were similarly unlateralized overall. Five of the 10 individuals showed no lateralization and no significant biases were seen in four of the 10 patterns. For the 63 testable (i.e., $N \geq 8$) combinations of category

[1]Yearly, these monkeys averaged only 17 percent of their time on the ground.

TABLE 2. Proportions of left/right hand usage and statistically significant binomial z-scores across subjects and behavioral categories

Subjects	Carry	Eat	Hit	Hold	Idle	Manip.	Reach	Retrieve	Self-groom	Social groom	Total	%R
Females												
01	15/13	164/198	1/0	396/367	168/163	8/1	1/1	115/103	7/21	19/29	895/896	50
03	6/2	172/305	2/4	447/298	191/180	10/40	2/4	115/99	12/7	13/12	970/951	50
		6.04		**−5.42**		**4.10**						
015	1/1	159/132	2/5	336/332	128/153	6/10	0/1	67/64	2/9	10/25	711/732	51
017	1/1	102/110	1/2	316/304	146/130	7/8	2/1	33/34	15/14	31/24	654/628	49
020	1/0	281/142	1/1	347/384	168/176	1/3	1/6	92/74	19/17	26/10	937/813	46
		−6.71									**−2.94**	
Males												
M11	1/0	139/78	0/0	343/376	194/194	3/2	5/10	51/35	11/10	0/10	747/715	49
		−4.07								**2.85**		
M24	1/3	186/44	0/0	221/331	152/159	2/0	4/3	59/27	4/6	0/0	629/573	48
		−9.30		**4.64**				**−3.34**				
M49	1/0	98/110	0/0	313/296	166/168	3/1	7/3	45/37	4/3	0/0	637/618	49
M69	1/0	174/174	0/0	386/362	127/149	2/6	1/0	71/45	2/14	1/0	765/750	50
									2.75			
M70	1/1	110/127	0/0	336/313	155/174	1/6	2/3	37/39	2/3	0/0	644/666	51
Total	29/21	1585/1420	7/12	3441/3363	1595/1646	43/77	26/32	685/557	78/104	100/110	7589/7342	49
		−2.99				**3.01**		**−3.60**				

$P < 0.01$ when $z \geq$ **2.58**; when z is positive, right preference, when z is negative, left preference; non-significant z scores are omitted.

and subject, only ten were statistically different from 50:50 (chance).

Only one of the females (O20) exhibited a significant degree ($z = -2.94$, $P = 0.003$) of laterality for her combined actions. Though this seems to suggest manual specialization, additional information makes it seem unlikely. First, looking at each of her behavioral categories separately shows that she exhibited hand preference only for Eat. That is, her overall score is not a true reflection of consistent laterality, but instead is an artifact of her very high Eat value biasing her overall score. Moreover, it is important to note here that on January 5, 1995 (5.5 months prior to the beginning of this study), O20 was observed to fall out of a tree 25 m high and completely break her right humerus such that she could not use the right arm for several weeks (Koenig, pers. comm.)

Similarly, the overall significant totals in Retrieve, Eat, and Manipulate are misleading. Scrutiny of Retrieve and Manipulate shows each to have only one significant individual. For Eat, five individuals showed higher right hand totals versus four with higher left hand totals, with one (M69) exactly ambilateral.

Though none of the behavioral patterns shows evidence of task specialization, the Eat and Hold categories are still noteworthy. For Eat, two females and two males of the 10 subjects showed significant degrees of hand preference ($z = 6.04, -6.71, -4.07, -9.30$; all $P < 0.0001$). Moreover, Hold seems to be complementarily associated with Eat in these subjects, especially for O3 and M24 (Fig. 1). That is, the requirements of the strata from which these monkeys eat require the associated holding (usually of the branch from which they eat) with the non-eating hand.

The data specific to Eat and Hold comprise: 1) six ambilateral subjects (three females, three males); 2) two subjects who Eat preferentially with the left hand, though their right hand doesn't perform a significant Hold (one female, one male); 3) one subject who Eats preferentially with the left hand and performs an associated Hold with the right (male); and 4) one subject who Eats preferentially with the right hand and performs an associated Hold with the left (female).

Using McGrew and Marchant's (1996) model of five levels of lateralization, the overall data from this study resemble Level 1 (all subjects ambilateral). The Eat data approaches a halfway point between Level 1 and Level 2 with approximately half the subjects significantly lateralized and the other half remaining ambilateral (Fig. 2).

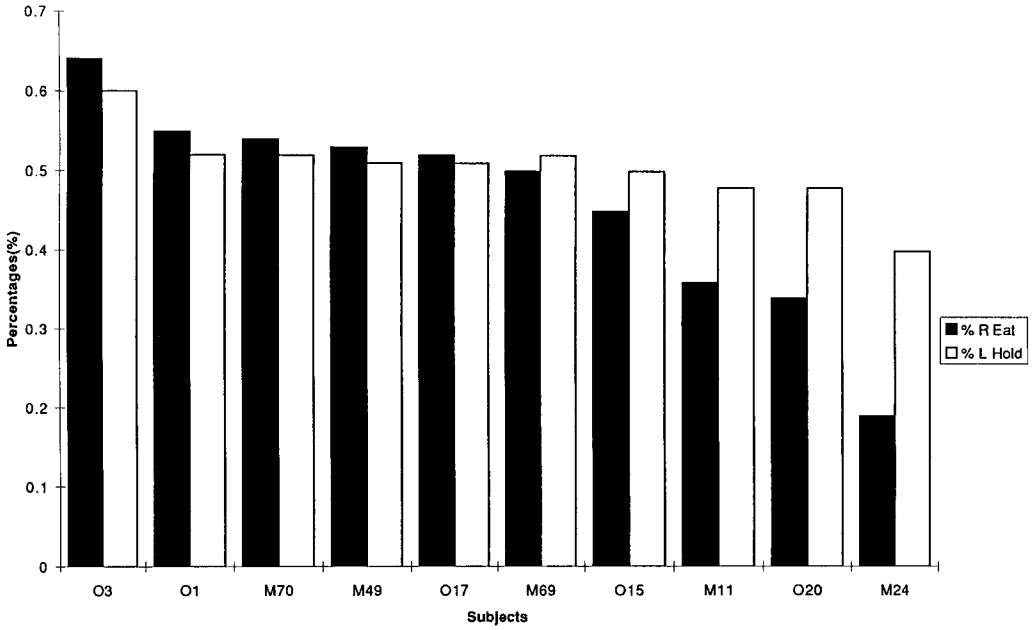

Fig. 1. Relative percentages of left holds and right eats by all subjects.

DISCUSSION

The observed trend is for a general lack of manual laterality in these langur monkeys, evidenced by the lack of substantial preferences in nine of the 10 categories. The only exception is perhaps for the Eat category in which four individuals showed a hand preference. Although our methods specifically took into account the recommendations of MacNeilage et al. (1987) regarding the conditions most likely to evoke manual asymmetries in nonhuman primates (wild study, separation of differing complexities of behavior, adult subjects), we found no evidence of population level handedness. Our data also conflict with MacNeilage et al. in that no right hand specialization for manipulation or postural support was seen (only one animal was significantly right-biased for Manipulate or for Hold).

It may be that complex, visually guided reaching offers the best chance of evoking manual asymmetries. But whereas MacNeilage et al. hypothesized that this asymmetry should be left-sided, we found only a greater asymmetry (toward both directions) in this than in other behavioral patterns. Our data seem to agree with Fagot and Vauclair (1991) in their separation of low-level and high-level tasks. As Eat is the most common visuo-spatial task of our repertoire, it would rightly be expected to display the greatest degree of manual asymmetry, but whereas Fagot and Vauclair claim that routinized behavior will not yield observable laterality, our results differ.

Eating is a highly visually oriented, yet routinized task for these monkeys, and the forelimb chosen is on average random on any given occasion. That is, there is no inherent asymmetry of the type envisioned by MacNeilage et al., in which there is an evolved manual specialization. It is not surprising that ambilaterality is preferred. In the three-dimensional environment of these monkeys, it is energetically sensible to remain maximally flexible rather than always to use one hand (see also Marchant and McGrew, 1996). Presumably, organisms in natural environments live in an unlateralized world. But, for a highly routinized task, a randomly chosen direction of laterality may become ingrained; at the very least,

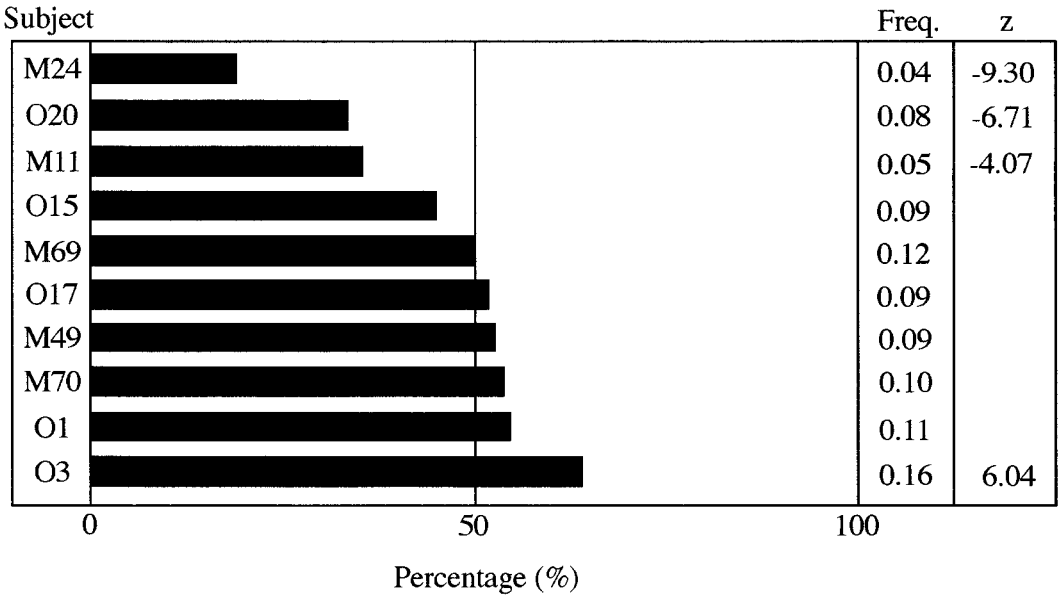

Fig. 2. Percent right hand Eat for each subject. Non-significant z-scores are omitted.

TABLE 3. Studies of laterality in reaching for food by adult colobines

Study	Species	Hand use				
		Left	Left/Right	Right	Ambilateral	Total
Mittra et al. (this study)	*Presbytis entellus*	3		1	6	10
Neves and Dolhinow (1994)	*P. entellus*		7		2	9
Yuanye et al. (1988)*	*P.* spp.	6		11	8	25
	Rhinopithecus roxellanae	3		5	4	12
Kubota (1990)	*Macaca fuscata*	10		3	2	15

* Ages not given.

this may cut down on decision-making time for an often repeated act.

The special case of O20 provides a unique chance to explore yet another plausible hypothesis for the random establishment of manual asymmetry. An arm injured during development (in this case completely broken from a fall) forced the consistent use of the alternate arm. This led to a significant overall, and specific categorical, laterality toward the direction of the noninjured arm. Such an "injured-arm" effect would still show up most clearly in a highly repeated behavior as the forced use of one hand over the other would most quickly ingrain itself in such a case. And, in fact, the only specific behavioral category for which O20 was significant was Eat. Thus, this randomization of asymmetry in a routinized behavior explains the overall Eat category being halfway between Level 1 and Level 2 of McCrew and Marchant's (1996) model of five levels of lateralization (see Fig. 2).

Also, in focusing on Eat, a clear discordance is seen between the results of this study and those by Neves and Dolhinow (1994), Yuanye et al. (1988), and Kubota (1990). These captive studies found differing degrees of manual asymmetry in a food reaching task (see Table 3), but in all cases except ours, the majority of subjects were lateralized and the minority were ambilateral. In our data set from the wild, ambilaterality is the norm, as for wild chimpanzees, *Pan troglodytes*, at Gombe National Park (Marchant and McGrew, 1996). This differs

from more lateralization seen in chimpanzees in captivity (Hopkins and Morris, 1993). What should also be noted is that the directionality of the preferences and the extent of the lateralization are inconsistent, even when comparing across adult subjects only. Therefore, one must be careful in extrapolating the results from studies of reaching for food to claims of evolutionarily prescribed laterality in a species. For colobines, until more data are collected, no generalizations within or across species are justified.

The results of this study emphasize the importance of looking at a variety of behavioral patterns of differing complexity (especially in species which do not exhibit tool use) in order to understand nonhuman primate manual asymmetries. Food reaching is an important pattern, but it is fraught with methodological complications, especially in captivity where food is usually presented in two dimensions on the substrate. One must be cautious in extrapolating data from food reaching studies to questions of species-level laterality. Its highly repetitive nature may force misleading lateralities in the subject. There is also a much greater risk of the observer failing to differentiate bouts and thus inflating sample sizes, which lead to statistically false positive results (McGrew and Marchant, 1996).

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